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# Aspen Stands as Wildfire Fuel Breaks

Gilbert H. Fechner and Jack S. Barrows

# ABSTRACT

    Fire ignition rates in quaking aspen stands are less than
half those for all other cover types in Colorado. These stands
do not support rapidly spreading or intense fires due to their
low burning index and spread component. Crown fires drop to
the ground when they reach quaking aspen stands, and prior to
autumn leaf fall, fire spreads only a short distance into the
stands.

    Quaking aspen propagation can be encouraged in the field
by severing roots from the main stem; under suitable tempera-
ture and light intensity, this stimulates abundant sucker
formation. Artificially, quaking aspen can best be propagated
through the use of root cuttings.

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## BACKGROUND

### Introduction

Quaking aspen (Populus tremuloides Michaux) is the most widely distributed tree species in North America, extending over 110 degrees of longitude from coast to coast, over 40 degrees of latitude from within the Arctic Circle to the northern tropics of Mexico, and from sea level to over 10,000 feet in elevation. Quaking aspen is a short-lived tree, maturing in 50 to 70 years in the Lake States and up to 125 years (rarely 200) in the Rocky Mountains (Stoeckler, 1960; Jones, 1967). In the mountainous West, quaking aspen constitutes an important watershed species, covering many acres of critical slopes; it is often the first species to return to a burned or heavily logged area, thus protecting the site until more tolerant, permanent species become established. Quaking aspen is also an important part of western forests as it enhances recreational values; the yellow, orange, and red autumn foliage provides one of Colorado's scenic attractions.

In Colorado, almost one-fourth of the commercial forest land, or about 2.0 million acres, is aspen type, the second largest in the State (Miller and Choate, 1964). Quaking aspen varies widely in size, quality, and vigor, attaining its best development for timber in the southwestern part of the State.

### The Problem

In mountain resort areas and many developing mountain communities, the potential increase of fire hazards and risks requires attention to specific measures for prevention of damaging forest fires. One of these measures may be the installation and maintenance of fuel breaks at strategic locations. However, fuel breaks need to be designed in a manner compatable with a combination of fire behavior, erosion control and aesthetic requirements. Establishment of stands of quaking aspen in fuel breaks may be a method of meeting these requirements.

### Purpose of the Research

The purpose of this research was to examine the feasibility of using natural or artificially-established quaking aspen stands as fuel breaks in areas of potential population build-up.

### Objectives

The potential use of quaking aspen stands as potential wildfire fuel breaks involves two important considerations: (1) the value of the species in reducing the occurrence and spread of wildfire, and (2) the ability to propagate this species successfully, especially on non-native sites. Hence, the specific objectives of this research were to:

a. Determine the needed locations, width, general configuration and vegetative characteristics of fuel breaks in mountain forest areas, from a fire, erosion control, aesthetic, cost and/or maintenance viewpoint.

b. Determine the probability for utilization of natural stands and propagation of new stands of quaking aspen on the type of sites required for effective fuel breaks.

c. Determine fire ignition, fire spread, general fire behavior and fire control factors in quaking aspen stands.

d. Analyze and evaluate the methods for the propagation and maintenance of quaking aspen stands under the soil, topographic and weather conditions of typical fuel break sites.

### Site Requirements

The widespread geographic distribution of quaking aspen, extending over much environmental diversity, reflects the great genetic adaptability as well as unusual ecological aggressiveness in this species.

In different parts of its natural range, quaking aspen endures winter minima as low as -78° F (-61° C) in interior Alaska and summer maxima of over +100° F (+38° C) near Fort Wayne, Indina. The growing season varies from 81 to 176 days (Strothmann and Zasada, 1957).

Extending from sea level to over 10,000 feet, quaking aspen in Wyoming reaches its lowest altitudes on northerly exposures and its upper limits on southerly exposures (Reed, 1971). In the Rocky Mountains, the lower altitudinal limit of its natural distribution coincides roughly with a mean annual temperature of 45° F (+7° C) (Fowells, 1965).

Quaking aspen grows on a wide variety of soils from rocky soils to heavy clays, but its growth and development are strongly affected by soil conditions. Best development occurs on porous, loamy and humic soils rich in lime. Good sites also are high in calcium, magnesium, potassium, and nitrogen, but mechanical properties of the soil are more highly correlated with growth than chemical properties are (Stoeckler, 1960).

Moisture conditions are favorable if the ground water level is less than 8 feet and more than 12 inches from the surface (Stoeckler, 1960). Growth on sandy soils is often poor due to low moisture levels, and it is poor on heavy clay soils due to poor drainage and consequent poor aeration. In some parts of its natural range, the presence of quaking aspen is associated with a sub-irrigated soil (Fowells, 1965).

Root development of quaking aspen is also strongly influenced by soil characteristics. Rooting depth in the Lake States is from 39 to 60 inches, although roots occasionally reach 85 inches. In the central Rocky Mountains a major limiting factor is the rockiness of the soil, hindering the lateral spread of the shallow roots and interfering with their tendency to rise close to the surface; this restricts the reproductive ability and general development of this species (Fowells, 1965).

A unique ecological habit of quaking aspen places this species in a highly competitive position in the plant community. Natural reproduction is primarily by suckering. Suckers develop from adventitious buds formed mostly during the current year along the small-diameter, shallow, lateral roots. These roots do not branch appreciably, and they extend as much as 80 feet from the parent tree or clone. The suckers grow rapidly, and ground cover is quickly produced (Barry and Sachs, 1968; Fowells, 1965; Sandberg and Schneider, 1953).

The great variation observed within this species in morphology, phenology, and autumn leaf coloration (Jones, 1967) and growth is displayed in clonal differences. Strain (1964) found ramets of one clone to average 11 feet in height, while those of another clone less than one mile away were 60 feet tall. He also found clones to vary in bark reflectivity. Leafing-out may vary by two to three weeks in nearby stands (Baker, 1921). The early-leafing trees, which also turn color earlier in fall, dominate at upper and middle altitudes in Utah (Morgan, 1969).

## Introduction

Until recently, quaking aspen was considered to be a weed species in American forestry. Little thought was given to its natural management; little thought was given to its propagation for artificial establishment. However, with an increased consumption of paper and paper products and a corresponding decrease in the availability of other suitable species, and due to its relatively rapid growth rate, more and more attention has been focused on the management of quaking aspen as a source of pulpwood supply. In fact, in 1953, quaking aspen was the principal pulpwood species produced in the Lake States, accounting for nearly 940,000 cords in that area (Horn, 1954). Furthermore, this species has become increasingly important as an ornamental tree. Hence, considerable research effort has been expended toward its genetic improvement and toward its propagation, both vegetatively and by seeds.

Quaking aspen belongs to the section Leuce Duby, one of five in the genus Populus L. (family Salicaceae Lindl.) Other members of this section include bigtooth aspen (Populus grandidentata Michx.), European white poplar (Populus alba L.), European aspen (Populus tremula L.), as well as a number of other species native to Europe and Asia (Rehder, 1940). A certain degree of similarity is accorded the members of this section in morphological, physiological and silvical characteristics. Thus, although this paper is intended to deal primarily with the propagation of quaking aspen (Populus tremuloides Michx.) and its several varieties and forms, certain information will necessarily be drawn from other members of the section Leuce Duby.

## Propagation by Seeds

Floral morphology

The flowers of quaking aspen develop from large axillary buds just below the terminal bud. Most commonly, they occur in the upper portion of the crown and on fully exposed branches in the lower portion of the crown (Einspahr, 1960; Lester, 1963). The flowers appear as drooping aments (catkins), in advance of the leaves, a relatively common feature among wind-pollinated angiosperms.

They normally appear in April or May although at high altitudes in the Rocky Mountains, they may not appear until June. Air temperature seems to be the principal factor affecting the time of flowering and the duration of the flowering period. A daily mean maximum temperature exceeding 54° F (12° C) for about six days appears to be necessary to initiate the flowering of quaking aspen in spring (Moss, 1960).

The individual flowers in the aments of both sexes are solitary, inserted on a cup-like disk and subtended by a pubescent, deeply-divided bract. The number of flowers in the pistillate catkin ranges from 90 to 100, each pistillate flower borne on a pedicel upon which the bract is also borne (Nagaraj, 1952). The pedicel, short at the time that the ovule is initiated, later elongates to about 2 mm and becomes rather conspicuous in the mature flowers (Fechner, 1972). When the stigmas are receptive, this disk surrounds slightly more than the lower one-half of the gynoecium (fig. 1), although in later development the disk is insignificant (Fechner, 1972). The ovary is always two-carpellate, although this feature varies in other species of the genus Populus L. Flowers in the staminate catkins range in number from about 80 to 100 or more (Nagaraj, 1952), each containing from 6 to 12 stamens.
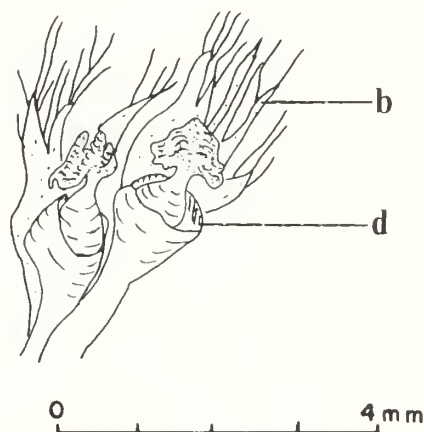


Figure 1.--Unpollinated pistillate flowers of quaking aspen at receptivity, showing relation of cup-like disc (d) and bract (b) to gynoecium (after Fechner, 1972).

At the time of pollination, the pistils are about 2 mm long, and they approximately triple in length as they mature. The hair-tufted seeds are then about 1.2 mm in length (Fechner, 1972).

Microgametogenesis - Staminate catkins of quaking aspen arise as buds during early summer. The young stamens soon become four-lobed, each lobe representing a microsporangium. The primary sporogenous cells within the microsporangia undergo several successive mitotic divisions, forming a group of micro-spore mother cells, 4 to 16 in any one micro-scopic cross-section (Nagaraj, 1952). As is true for other species of Populus L., as well as for many other genera and families, the staminate catkins overwinter in the spore mother cell stage (Smith, 1943).

The following spring, the microspore mother cells undergo meiosis rapidly, im-mature pollen grains developing within 24 to 36 hours after the first meiotic division takes place. Instigation of the meiotic division is usually correlated with the development of anthocyanin in the anthers (Smith, 1943).

The resulting four microspores of the tetrad are usually tetrahedral in arrangement. However, cell wall formation takes place by a furrowing process, which is easily upset and may result in the formation of dyads instead of tetrads. If cell walls fail to form between the two meiotic divisions, the dyads will then be binucleate. Also, occa-sionally, three or five microspores result from meiosis of a single microspore mother cell, instead of the usual four (Smith, 1943), presumably also due to an upset of cytokinesis. There is some question as to the fertility of these microspores, however, Ordinarily, within each microspore, the nucleus divides to form a generative nucleus and a tube nucleus, the pollen being shed in this condition (Nagaraj, 1952).

Megagametogenesis - Pistillate catkins arise in buds toward the end of the summer. In the Chicago, Illinois area, the ovaries show no trace of ovules yet in August, but ovules are conspicuous in October (Nagaraj, 1952). Initiation of the gynoecium can be detected, however, as early as the end of June (Lester, 1963). The primary sporogenous cell in the ovule enlarges considerably to become the megaspore mother cell. The first division of the megaspore mother cell pro-duces a dyad, following which both members of the dyad divide again to form the tetrad, usually linear in arrangement (Nagaraj, 1952).

Immediately following tetrad formation, the three micropylar megaspores begin to degenerate, while the chalazal megaspore en-larges (Nagaraj, 1952). Thus, female game-tophyte development is monosporic; and it is of the Polygonum type, common among angio-sperms. The degenerating megaspores persist until the functional one has divided once, but they disappear during the 2-nucleate stage; the condition of the gametophyte, when the pistil is receptive (fig. 1) at pollina-tion (Fechner, 1972). The early 4-nucleate gametophyte is still enclosed in the nucellus, but before the third division occurs (between the 4-nucleate and 8-nucleate stages), the gametophyte elongates rapidly. It penetrates the micropylar end of the nucellus and pro-jects into the micropyle itself. This pene-tration apparently takes place by digestion of nucellar tissue by the gametophyte. Organ-ization of the embryo sac takes place rapidly after the 8-nucleate stage has arrived (Nagaraj, 1952; Fechner, 1972).

In the early stages of development, the nucellus tissue increases in size very rapidly, but later it apparently serves as nutritive material for the developing embryo sac (fig. 2).
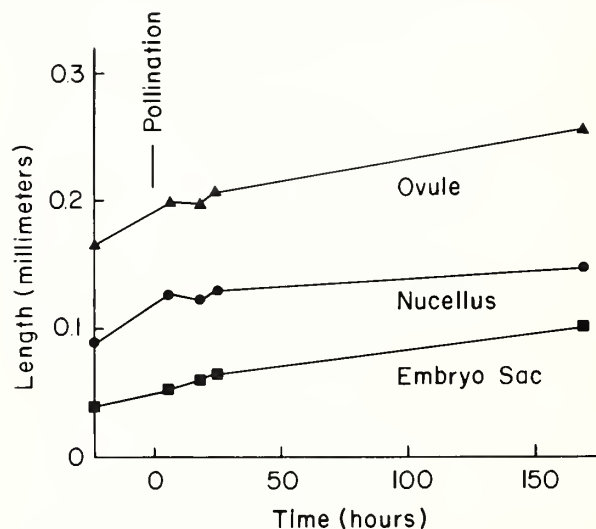
Figure 2.--Average length of components of unfertilized quaking aspen ovules, unpol-linated and at different times following artificial pollination in the laboratory.

Fertilization and seed development - The process of fertilization is regular. Prior to entrance of the pollen tube, the polar nuclei fuse to form a 2n fusion nucleus. The pollen tube enters the micropyle, and double fertilization takes place. About the time of entrance of the pollen tube, the synergids break down, and shortly after

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fertilization, the antipodals also disappear (Nagaraj, 1952). In the laboratory (25° C), fertilization occurs within 3 to 5 days after pollination (Fechner, 1972); it occurs in 10 to 12 days after pollination in the field (Fechner, 1975).

Very rapid development occurs in ovules following fertilization. The developing seeds reach about 1 mm, or about three to four times the length of unfertilized ovules, 168 hours after pollination in the laboratory (Fechner, 1972). By this time the early globular embryo is visible in the micropylar region surrounded by free-nuclear endosperm (fig. 3). Unfertilized ovules within ovaries containing one or more fertilized ovules develop normally for one week after pollination in the laboratory and in the field, reaching the mature embryo sac stage, but they degenerate soon thereafter.



Figure 3.--Early embryo and free-nuclear endosperm, 168 hours after pollination (820 X).

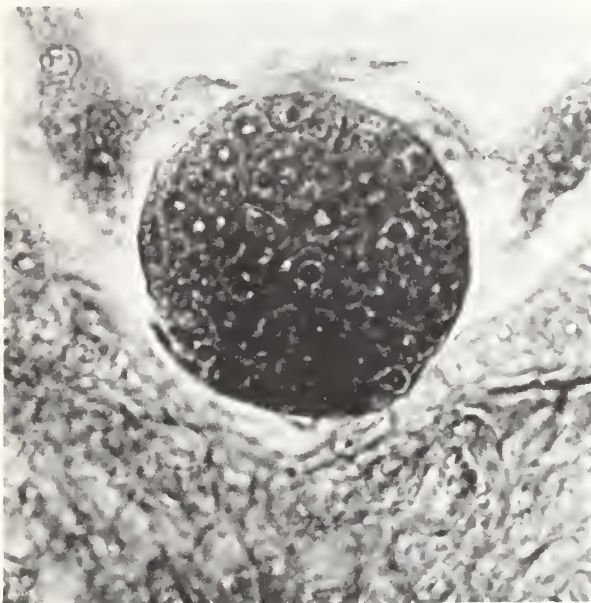About the time that the ovules reach their mature size, hair cells develop. These hair cells originate on all sides of the surface cells of the funiculi regardless of whether the ovule is fertilized (Fechner, 1972, 1975). These hair cells develop into the tufts of silky hairs (coma) by which the pear-shaped seeds are air-borne when released from the capsules. Since the hairs are not an outgrowth of the seed coat, they are not truly seed hairs (Maini, 1968a).

Under laboratory conditions, viable seeds are produced in about two weeks (Fechner, 1972), although four to six weeks are normally required in the field (Fowells, 1965). The mature seeds are slightly over 1 mm in length.

This maturity is reached when the new leaves are about 2 cm in diameter. Seed dispersal reaches 400 to 500 meters (Stoeckler, 1969).

Flowering age in quaking aspen is usually about 8 to 10 years (Stoeckler, 1960); the author has observed a female tree of sucker origin to flower at four years. Flower and seed production may be very high. A single 23-year-old, 33-foot tall individual, located about 60 miles north of Toronto, Ontario bore approximately 900 productive shoots, 2200 catkins, 170,000 capsules, and 1,625,000 seeds (Maini, 1968a).

Sex ratio - In most dioecious organisms, males and females occur in approximately equal proportions in the population. This is predicated on the idea that sex is gametically controlled, that the gametes and subsequent zygotes are equally viable, and that no selection or other pressure is operating against either sex. Thus, it is not surprising that considerable interest should be displayed in the ratio of the sexes in aspen and in the sex determination mechanism.

At a very early date, Baker (1918) observed that in the Rocky Mountains, pistillate trees of quaking aspen occupied only a small portion of the aspen type, but no counts of trees of the two sexes were made at this time. Pauley (1948) found that of 76 clones of a number of different species of Populus, including quaking aspen, 23.7 percent were female, and in another study, conducted on a seedling population in northern Minnesota, it was found that 28.2 percent of the quaking aspen trees studied were female or predominantly female (Pauley and Mennel, 1957). Thus, an approximate 3:1 ratio could be inferred from these data. However, Einspahr (1960b) found that among 91 quaking aspen trees examined, the proportion of males to females did not differ significantly from a 1:1 ratio.

Pauley (1948) indicated that the 76 clones of Populus referred to above were selected on the basis of good form and vigor, and he suggested that perhaps there is an association between sex and such characteristics, and that vigor may operate as a selective force in favor of males. Einspahr (1960b) was unable, however, to associate any characteristics that he studied with either of the sexes in quaking aspen, although vigor per se was not one of these characteristics. Blake, et al. (1960) correlated extracts from mature leaf buds from 20 quaking aspen trees with the sex of the tree from which the buds were taken, using descending paper chromatographic techniques. However, in another population of 200 trees this work could not be duplicated (Blake, et al., 1967).

Hermaphroditism - The entire question of sex in aspen is complicated by the fact that the dioecious nature of the species is not a consistent one; hermaphroditism has been regularly observed. Hermaphroditism refers to the presence of both sexes in one individual, in different ways: (1) male and female flowers borne separately on a single tree (monoecism), (2) male and female flowers separate but on the same catkin (bisexual catkin), and (3) male and female parts in the same flower (perfect flower) of a catkin. Apparently all types occur in quaking aspen and related species (Schlenker, 1953; Einspahr, 1960a). Sometimes the distribution of the unisexual and bisexual flowers varies markedly among branches of a single tree (Maini and Coupland, 1964; Stettler, 1966). Erlanson and Hermann (1927) found variation within a catkin from all male flowers (1 percent of the catkins examined) to all female flowers (17 percent). The remaining catkins examined contained some flowers of each sex.

Schlenker (1953) prepared the following classification of aspen trees, with respect to their sex, based on his studies with Populus alba L., Populus tremula L., and Populus tremuloides Michx.: (1) pure females; (2) predominantly female, slight androgynism; (3) pure males; (4) predominantly male, slight androgynism; (5) strongly developed androgynism.

Erlanson and Hermann (1927) found that male and female organs in perfect quaking aspen flowers developed normally. The stamens were typically attached to the inner walls of the cup-like disk, and there were no anthers on stigmas nor anthers on carpels. The same authors found that the number of stamens in these perfect flowers was about 1/4 that in flowers on normal male trees. However, Seitz (1953) also found that the gynoecia develop normally in hermaphrodite flowers of European aspen, as they do in the female of dioecious trees.

Schlenker (1953) noted that the result of a cross between a European aspen (Populus tremula L.) female and a European white poplar (Populus alba L.) male yielded predominantly female progeny. But the reciprocal cross produced either 3/4 pure male and 1/4 female or predominantly female progeny, suggesting, perhaps, some type of dominance of aspen over poplar.

Pauley and Mennel (1957) showed that about 5 percent of the male or predominantly male trees of quaking aspen studied had bisexual flowers, while about 20 percent of the female or predominantly female trees had bisexual flowers. Santamour (1956) found that of 300 female trees examined, almost 50 percent bore some male flowers. But he felt

that this figure was conservative, because he sampled only 10 catkins per tree, and in many cases, only one catkin of the 10 contained bisexual flowers. It is conceivable that all aspen trees have both male and female potentialities.

Pollen obtained from hermaphrodite trees by Erlanson and Hermann (1927) averaged about 30 percent larger in diameter than that from normal quaking aspen, and Seitz (1953) felt that the occurrence of uninuclear gones and single gones containing two to four nuclei may have explained the greater variability in diameter of pollen from European aspen hermaphrodites compared to that from normal trees. Pollen size has not been adequately explained.

Erlanson and Hermann (1927) found that pollen obtained from hermaphrodite flowers was effective in self-fertilization, but it was ineffective in fertilizing normal female quaking aspen (Populus tremuloides Michx.). This is indeed puzzling. The seeds obtained from self-fertilized plants produced seedlings, but it is not known what survival was obtained.

However, Seitz (1953) found that in European hermaphrodites, some pollen mother cells did not develop beyond early prophase, because synapsis failed to occur. More commonly, however, tetrads developed, as did pentads and hexads. He further found that in self-fertilization, irregularity occurred, the pollen tubes often not reaching the ovule. He did not report obtaining viable seedlings.

Sex determination - Of the several sex-controlling mechanisms known in nature only one has been investigated in aspen. This is the X-Y mechanism, in which one of the sexes contains a heteromorphic pair of chromosomes (X and Y), one of which is considered to be the sex chromosome. Thus, with distribution of the members of this pair to opposite poles at meiosis I, gametes have either the X or the Y chromosome, and subsequent zygotes have either the heteromorphic pair or the sex chromosome in duplicate, and the sexes will occur in a 1:1 proportion.

Working with Populus tremula L., Blackburn and Harrison (1924) noticed, at both divisions of meiosis, a single chromosome, which was equal to or larger than the volume of any other two. This chromosome was compound in structure and appeared four-lobed. The investigators took this as evidence that heterochromosomes exist in this species and that they possibly were sex chromosomes.

Erlanson and Hermann (1927) also felt that they found eighteen pairs of autosomes and an unequal sex pair at metaphase I in the pollen mother cells of Populus tremuloides Michx. Thus, they apparently felt that if sex were determined by the X-Y mechanism, the male sex would have the heteromophic pair. Later workers (Peto, 1938; Johnsson, 1940), however, have been unable to verify heteromorphic chromosome pairs in the aspens. And attempts to correlate morphological features with the sex of the tree have not proved fruitful. Thus, at present, the mechanism of sex determination in quaking aspen is not known.

Factors Influencing Flower Development

Little is known about the external factors affecting flowering and fruiting in quaking aspen, as in many other forest tree species, due in part to the large size of sexually mature individuals. This size precludes their study under closely controlled conditions, such as may be obtained in greenhouses and growth chambers. However, some effects of external factors on the flowering of quaking aspen can be speculated from impressions gained through indirect observations.

Temperature - Seitz (1958) collected twigs of a male European aspen weekly from August to December. Some twigs of each collection were placed in cold storage before being forced in the greenhouse. Control twigs of each collection were placed in the greenhouse without prior cold treatment. Results were variable. Whereas, twigs collected in August and subjected to +4 degrees Centigrade in the dark produced pollen, the controls of the same collection produced none. But twigs collected in October and subjected to +4° C produced no more pollen than did the control twigs.

Male and female branches of quaking aspen trees in Saskatchewan, which were brought indoors in mid-January and maintained at room temperature, flowered in 10 days (Maini, 1968a). In our own experience with quaking aspen in Colorado, branches collected in February, 1975, produced 100 percent aborted pollen grains. In later collections, pollen was readily forced in the laboratory. The date after which forced pollen was readily obtained varied with the altitude of the donor tree, but it was usually associated with the extension of the catkin bracts through the tips of the bud scales by about 3 to 4 mm. Artificial pollination in the laboratory of forced female and male quaking aspen collected just before anthesis has been reported (Einspahr, 1969; Fechner, 1972).

Hence, it would appear that some variable period of low temperature is required to induce flower development of quaking aspen after the flower buds arise in the summer. In other words, dormancy is not broken until the low temperature period has been effective in bringing about such changes as permit resumption of development. But no information is available on the effect of temperature on the stimulation or induction of floral bud formation in early summer.

Pauley and Perry (1954) felt that break of dormancy of black cottonwood (Populus trichocarpa Torr. & Gray) in spring was also controlled mainly by temperature, although they observed only vegetative growth. However, it has become common practice among investigators to retard or speed up the development of flowers on twigs under laboratory conditions by controlling temperature, in order to have male and female flowers developed at the same time for artificial crossing purposes. The exact role played by spring temperature in the development of quaking aspen flowers is not known.

Chemical treatment - Larsen (1958) found that 1/4 percent and 1 percent concentrations of gibberellic acid by weight in lanolin stimulated flower development of Populus tremuloides Michx. and Populus grandidentata Michx. Application was to terminal wounds of twigs which had been placed in water in the greenhouse. Treated cuttings broke dormancy several days before the controls and they attained about three times the length of the controls. Pollen shedding time, however, was not affected by the treatment.

Physical treatment - A relatively few studies have been designed to promote the development of flowering buds on aspen. Such studies have necessarily been conducted on trees in an outdoor environment. Einspahr (1960b) has obtained some success by girdling Populus tremuloides Michx. trees in Wisconsin and Michigan, but no quantitative figures have been seen which would indicate the degree of stimulation that he obtained.

In this connection, Heimburger (1951) grafted root sucker scions of European aspen of a Polish source into the crown of a dwarf variety of Populus tremuloides Michx. occasionally found in southeastern Canada. During the first year, the grafted portion produced juvenile, sucker-like growth. However, in the second year, this scion material developed adult-like foliage, and flower buds formed in the axils of some leaves.

Production of Seedlings

Large quantities of seed are produced about every 4 or 5 years (Strothman and Zasada, 1957), and the germinability is high, though normally of short duration -- usually 2 to 4 weeks in nature. Strain (1964) obtained 95 percent germination with 38 hours from seeds that had been stored for 115 days at 40° F (4.4° C) and Morgan (1969) obtained 79 percent germination after 1-1/2 years of storage at about the same temperature (3.3° C). The seeds are not dormant and germination occurs in one or two days on a moist seed bed, at any temperature between 32° and 95° F. although Morgan (1969) obtained poor results at 2.2 to 3.9° C. Germination does not depend on light (Fowells, 1965).

The primary root of a young quaking aspen seedling grows very slowly for several days, and during this critical period the plant depends on a brush of long, delicate hairs to perform the absorptive function, attaching to the uppermost soil particles, leaves, or decaying vegetable matter (Barnes, 1966). These hairs, first described by Yanchevsky in 1904 according to Moss (1938), arise from the junction of the root and the hypocotyl, and although they provide a large absorbing area, they are effective only if the surface is moist; drying of the uppermost soil or litter layer soon causes death of the seedling. Occasional natural quaking aspen seedlings are found and their verification is reported (Ellison, 1943; Strain, 1964; Jones, 1974b). Seedlings may eventually reach a height of 12 inches or more during this first year and develop an 8- to 10-inch taproot. During the second and third years, widespreading lateral roots are developed. Yet, although quaking aspen seedlings are occasionally reported, their establishment in nature is rare.

The paucity of quaking aspen seedlings in nature is attributed to one or more of several factors (Maini, 1968a):

1. Short seed viability.

2. Presence of a water-soluble germination and growth inhibitor in the "seed hair" (coma).

3. Unfavorable moisture conditions during seed dispersal on upland sites that aspen usually inhabits.

4. Susceptibility of seedlings to high temperatures that occur at the soil surface, especially if blackened by fire.

5. Susceptibility to fungi.

6. Unfavorable chemical nature of some substrates.

What may be a typical pattern of quaking aspen seedling performance in the field is documented by Strain (1964). A total of 52 seedlings were found on moist mineral soil in east-central California and marked on July 7. At this time the upper 1/2-inch (1 cm) of soil contained 26.8 percent moisture. Nine days later, the soil moisture content had dropped to 3.4 percent, and only three wilted seedlings remained; all were dead by July 23. In another locality, Strain found two of nine original seedlings to persist about two months, but they too died by early October.

Quaking aspen seedlings are produced in commercial quantities in Wisconsin. Best results are obtained if the seedbed is never allowed to dry, yet is never puddled during the first two weeks following seeding and if the seedbeds are fumigated in spring before seeding with methyl bromide and treated with the fungicide captan regularly through July to control damping-off (Benson and Dubey, 1972).

Vegetative Propagation

Suckering in Natural Stands

In addition to occasional seedlings, quaking aspen regenerates infrequently by root collar sprouts and less often by stump sprouts on young quaking aspen up to sapling size. However, most natural regeneration in quaking aspen occurs as root suckers. For example, when a five-year-old quaking aspen stand was slashed, the stand regenerated vegetatively: 6 percent stump sprouts; 12 percent collar sprouts; 82 percent suckers (Maini, 1968a). And this suckering characteristic is so common that the clone, rather then the individual tree, is the unit of study and the unit of genetic diversity. Clones vary greatly in size. In Michigan, clone size is apparently inversely proportional to the number of seedlings that become established, averaging less than 1/10 acre (Barnes, 1966), whereas the Canadian Forestry Service (1974) has reported that clones may spread as large as three or four acres.

Quaking aspen has a very shallow, widely-spreading root system. Four or five strongly-developed lateral roots originate at the root collar, taper rapidly, and branch within less than one meter. Cord-like branch roots radiate outward parallel to minor contours of the surface of the soil (Sandberg and Schneider, 1953) or even a stump substrate

(Jones, 1974a). Anchorage is provided by a few vertically penetrating roots, originating at the base of the tree and by "sinkers" arising from the lateral root system (Maini, 1968a). These cord-like lateral roots, often less than two centimeters thick, extend for varying distances with little taper; they may reach to 80 feet (24 meters) from the parent tree or clone. The majority of the roots are found in the top four feet (1.2m) of soil, although some sinker roots may reach 114 inches (2.8 m) in sandy loam and 50 inches (1.2 m) in clay (Sandberg and Schneider, 1953; Gifford, 1966; Barry and Sachs, 1968; Maini, 1968a).

Within clones, the pattern of the root system is variable. Gifford (1966), tracing parent trees (ortets) and their ramets with translocated dye, found that some ramets had no root development whatsoever other than the parent root from which they originated, and some had only a single vertical or lateral root developed. In other instances, ramets form their own root systems rapidly, and death of ramets and decay of root connections may thus result in the formation of several independent root systems within the same clone (Barnes, 1966).

The root suckers are produced from buds on the shallow roots, usually on those within 2 to 12 inches of the surface (Gifford, 1966). Sandberg and Schneider (1953) found 60 percent of them originating within one inch of the surface in humus or mineral soil, and small increases in depth inhibited suckering. A marked thickening of the parent root usually takes place on the distal side of the sucker, suggesting that food material produced in the sucker is translocated toward the growing tip of the root (Strothmann and Zasada 1957).

Morphogenesis of suckers.

Root suckers develop from adventitious buds[1] arising in the root phellogen (cork cambium). In quaking aspen the phellogen orgiinates in the pericyle (Brown, 1935). Initially, there is a small nidus of meristematic cells just within the cork; eventually, vascular connection with the conducting system of the root is made (fig. 4).

Sandberg and Schneider (1953) observed that although suckers could arise from suppressed buds, 95 percent of successful suckers

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[1] Adventitious buds are those produced in parenchyma tissue not directly associated with apical meristems and the places not dictated by their normal phyllotactic patterns (Zimmermann and Brown, 1971).
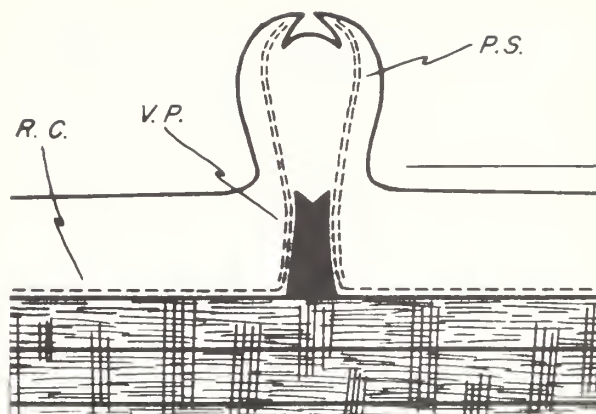


Figure 4.--Adventitious sucker bud. Vascular connection between the bud and the root. (P.S. = procambial strand; V.P. = vascular peg; R.C. = root cambium.)(After Brown, 1935.)

originated from buds initiated during the current year. Furthermore, the suckers from the new buds were more vigorous than the others. Suppressed buds are previously-formed buds embedded in the periderm or outer bark. The periderm consists of the phellogen or cork cambium,the phellem or exterior layers, and the phelloderm or cortical parenchyma. These suppressed buds are active during much of the growing season, in laying down new primordia and in keeping pace with the radially-expanding cambium (Zimmerman and Brown, 1971). It is now believed that suckers do not originate from suppressed buds in the periderm; rather they originate from pre-existing or currently-initiated shoot primordia.

Primordia on quaking aspen can best be observed if the phellem is peeled from the root. The most immature primordia macroscopically visible look like ellipsoidal masses of cells. At their most advanced stage of development pre-existing primordia form a rounded mound of relatively high tissue organization (Schier, 1973a). It is possible that pre-existing primordia on roots may be indeterminate until physiological conditions dictate whether they should be shoots or roots (Schier, 1973a). Adventitious shoot (sucker) development thus consists of two phases: development of a meristem, and shoot outgrowth (Schier, 1973a).

Factors Affecting Sucker Production

Apical dominance - Sandberg and Schneider (1953) observed that although several suckers often arise in a short distance of root, one soon dominates the others. To test the implications of this observation, Farmer (1962) severed all lateral roots from 1 to 2 feet

(0.3 to 0.6 m) from the parent tree. This root pruning stimulated suckering from the detached roots, whereas root segments still attached to the main stem produced no suckers. These results are considered as evidence that apical dominance is a factor in controlling suckering. Furthermore, removal of apical buds of suckers from root cuttings has also been found to increase the number of subsequent suckers produced. Stoppage of shoot growth by short-day treatment had a similar stimulating effect in inducing abundant suckering. These treatments produced a corresponding decrease in the auxin content in the roots (Eliasson, 1971c: Schier, 1972).

Auxins - Auxins (hormones), such as IAA (indoleacetic acid) are bud inhibiting (Zimmerman and Brown, 1971). Girdling of the stem by removing a band of bark, or cutting into the stem to sever the phloem and cambium usually releases suppressed buds (or pre-existing or currently-initiated shoot primordia) from inhibition below the girdle or wound. This response is usually accepted as evidence that the inhibition has been removed by blocking the downward movement of auxin. Farmer (1962) inhibited sucker formation with an IAA lanolin paste on intact root systems of 1-year-old quaking aspen. Schier (1973b) derived extracts from quaking aspen roots at different times of the year, from shortly after bud burst in May until 2-1/2 weeks after leaf fall in October. He found that auxin was highest in June and sucker development declined then. Furthermore, Schier attributed 72 percent of the variation in sucker numbers to auxin content. Eliasson (1971b) had found similar patterns in European aspen. The capacity to form suckers was low, and the auxin level was hgihest, during the period of shoot growth, showing that suckering in roots of intact aspen plants is prevented by auxin transported into the roots from growing shoot parts. These results seem to substantiate the field observations of Barry and Sachs (1968), who reported maximum sucker production in late spring and early summer, as the snow thaws, in the Lake States, presumably before active translocation of auxin. Eliasson (1969) had previously found that high levels of auxin in European aspen stem tissue corresponded with growth inhibition of _Avena_ in bioassay.

Temperature - One year following cutting, Shirley (1931, 1932) found a sharp increase in the number of suckers on clearcut versus partially-cut or uncut plots. He also found that burned clearcut plots had 30 percent more suckers than unburned plots. He attributed this difference to the increase in heat absorption of the blackened surface. Maini and Horton (1966a) found that burning,

scarification, and cutting all stimulated quaking aspen suckering. The response was greater on cut than uncut plots and greater for moderate than for light treatments. The treatments also produced increased surface soil temperature. From this and later study, the authors felt that the principal effect of cutting practices on increasing suckering was that of influencing the increased solar radiation and temperature on the forest floor. Strothmann and Zasada (1957) reported 1980 suckers per acre following cutting of a 43-year-old stand to a 10-inch diameter limit, 2115 to a 9-inch diameter limit, 4500 to an 8-inch limit and 6830 on a clearcut.

Light intensity - Sandberg and Schneider (1953) found no difference in suckering in full light, 50 percent, 25 percent, and no direct light on the soil surface in greenhouse tests. When sucker formation from root sections was compared in the light and in the dark, no difference in numbers was found (Eliasson, 1971a), but the inhibitor fraction (RF 0.4-0.7) was 10 times more active in the light-grown than in the dark-grown shoots. However, quaking aspen is very intolerant, and a reduction in light intensity affects very early growth and development of the young suckers. Those stems that fall below the general level of the crown stop growing and die within a year or two; in one study, 1/8 as many stems remained after seven years as after two years following cutting (Strothmann and Zasada, 1957).

Photoperiod - No studies have been seen in which photoperiod has been related to the production of suckers nor where its manipulation has been attempted for the control of sucker initiation. Yet, it is known that the photoperiodic response mechanism involves the production and translocation of one or more growth hormones (Kramer and Kozlowski, 1960). Long days, for example, are associated with high auxin levels in some tree species, while short days favor lower levels of the hormone.

Developing buds and mature leaves have been shown to be the organs sensitive to the day length stimulus as well as the sites of auxin synthesis (Kramer, and Kozlowski 1960). The induction of cambial growth by hormones produced in expanding buds in the spring is often cited as an example of hormone control of growth (Kozlowski, 1971a; 1971b; Perry, 1971).

Suckering in quaking aspen is also known to be related to auxin level, and sucker production has been shown to be correlated with the seasonal levels of auxin (Eliasson, 1971c; Schier, 1972, 1973b). Furthermore, the genus _Populus_ is known to exhibit genetic variation

in response to the photoperiodic stimulus: quaking aspen of a Saskatchewan source was rendered dormant by short day treatment (Pauley and Perry, 1954; Vaartaja, 1960). An important area of research, therefore, seems to be that of controlling photoperiod in an attempt to control sucker production through auxin manipulation.

Carbohydrates - In Utah and Alaska, the seasonal trend in total nonstructured carbohydrates was low during spring and early summer, increased rapidly in July, peaked around September and then decreased during autumn. Sucker numbers were not correlated with T.N.C. (Schier and Zasada, 1973). However, Strothmann and Zasada (1957) had reported that if all new suckers are destroyed by cutting or heavy grazing for three successive seasons, suckering usually ceases.

Age - The suckers of quaking aspen borne on the young, distal portions of the root system are the most recently formed, and they ordinarily become progressively older as the older parts of the root are approached toward the parent tree, but sometimes young suckers are found right next to older ones (Brown, 1935).

Fire - When a quaking aspen stand, or a conifer stand containing considerable aspen is severely burned, sucker density after the first full growing season may be tens of thousands per acre (Jones, 1974b). Repeated fire also increases the number of aspen sprouts, although the sprouts are less vigorous than those following initial burning (Perala, 1974). Most authors consider the effect of fire on increased sucker production as an indirect one, the fire affecting surface soil temperature or causing injury to the parent trees.

Injury - Large numbers of primordia on the roots of quaking aspen are often associated with injury such as grazing, which may have upset the hormonal balance, such as a temporary decrease in auxin levels (Schier, 1973a). Presumably, fire in an aspen stand could similarly upset the hormonal balance.

Artificial Propagation

The natural suckering habit of quaking aspen has stimulated a great deal of research in its vegetative reproduction by artificial means. Attempts have been made to perpetuate this species through hardwood or softwood stem cuttings, root cuttings, grafts, and tissue culture techniques.

Tissue culture - The establishment of plants on artificial culture media, from small pieces of tissue from those plants,

provides an opportunity for multiplication of individuals on a large scale within a small area. It also provides a supply of genetically identical material for study under closely-controlled conditions. The development of callus tissue is uaually a precursor to the development of a new plant by these culture techniques.

Mathes (1964) found that the growth of callus tissue obtained from stem segments of quaking aspen on a nutrient-base culture medium was improved somewhat with the addition of casamino acids or 0.5 ppm IAA, and it was more than doubled with the addition of 0.5 ppm NAA (naphthaline acetic acid). Friable callus tissue, initiated from segments of root-sprouts of this species, has also been grown on a 2, 4-D agar medium. Such tissue grew faster when subjected to occasional light than if grown continuously in the dark. And under 16 hours of light per day, this tissue turned red in color (Winton, 1968a; 1968b), suggesting the presence of some photoresponsive pigment.

Callus tissue of quaking aspen root-sprout origin has produced roots when the tissue was transferred to an agar medium following one to three months in a liquid nutrient medium (Winton, 1968c). Ultimately, after two years of development on artificial media, multiple stunted shoots and a few vigorous shoots have been obtained, and the new plants have become self-sustaining in a semi-sterile soil (Winton, 1970).

Grafts - Relatively little grafting has been attempted in quaking aspen. One example, however, is the bottle graft. In this technique, branches bearing flowers are placed in jars of water in the greenhouse and are united, in a manner of an approach graft, with the stem of a potted seedling of the same species. When the union is complete, the base of the scion is pruned off close to the union producing a "dwarf tree" which may continue to flower for several years (Pauley, 1949). Such grafting of male and female parts to form a single "dioecious plant" could provide unique material for genetic study.

In another example, success has been reported in the grafting of quaking aspen scions onto short, unrooted cuttings of balsam poplar or willows. The latter stock roots easily, and later, the aspen scion also roots (Strothmann and Zasada, 1957).

Stem cuttings - Most members of the genus Populus, especially the balsam poplars and the cottonwoods, are easily propagated by the rooting of stem cuttings, but quaking aspen is difficult to propagate in this way

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(Maini, 1968a; Sekawin, 1969). Factors affecting the variable success are discussed below.

Root cuttings - Whereas, the rooting of quaking aspen stem cuttings is generally difficult, greater success has been achieved through the use of root cuttings in different ways (Barry and Sachs, 1968; Starr, 1971; Zufa, 1971):

1. Suckers with intact roots have been lifted from stands and used as transplants.
2. Roots of a known tree have been used directly as root cuttings.
3. Softwood stem cuttings from sucker sprouts taken from root cuttings have been subsequently rooted.

Factors affecting propagation by stem or root cuttings

A number of factors are known to affect the success of rooting of stem cuttings taken from sucker sprouts and other branch material or of root cuttings, under greenhouse and laboratory conditions. These include soil medium, temperature, time of collection of root cuttings, length of storage prior to planting, and hormones. In addition, a great deal of variation in success exists among clones.

Soil medium - Various media have been used successfully for propagating root or stem cuttings, including vermiculite, perlite, sand, and soil, as well as combinations of these. When comparisons are made, variable results are obtained. For example, Sekawin (1969) felt that sand was less favorable than other media, but other workers found sand and 1/2 sand - 1/2 soil to be superior to soil alone (Starr, 1971). Root cuttings resuire aeration, however; in saturated or flooded soil, the cuttings decay (Maini, 1968a).

Temperature - Under natural conditions, sucker initiation is apparently favored by an increase in soil temperature occasioned by cultural practices. Similarly, under controlled conditions, Maini and Horton (1966b) found that maximum numbers and maximum growth of suckers from root cuttings occurred at 74° F (23° C), declining gradually above and below that temperature, within the range of 58° F to 95° F (14° to 35°C studied. Zasada and Schier (1973) found that a maximum/minimum temperature regime of 20°/10°C was decidedly poorer than either a 25°/15° C or a 30°/20° C regime in the number of suckers produced from root cuttings. Sekawin (1969) also reported that the optimum temperature for the rooting of stem cuttings is between 20° and 30° C.

Time of collection - The date on which root cuttings are taken affects the number and size of suckers produced, but results have been variable. On the one hand, Starr (1971) obtained similar numbers of suckers on root cuttings from four different collection dates between June and September, slightly higher than average in June. Zufa (1971) found that root cuttings planted in the fall began suckering 25 days later, and the 2- to 4-day-old suckers rooted 84 percent. Whereas, roots planted in the spring began suckering in 12 days, but only 48 percent rooted. Zasada and Shier (1973) also found that the date of collection had a significant effect on the numbers and dry weights of suckers per root cutting from three Alaska clones. On clone produced its greatest number of suckers from roots collected in June, the other two from roots collected in August or October.

Hormones - Considering the principle that growth regulators are trans-located within the plant and apparently affect sucker and root initiation, it is not surprising that their use would be attempted in promoting the rooting of stem cuttings. Ordinarily, low levels of kinitin (6-furfur-aminopurine), a DNA derivative, and high levels of auxin (indoleacetic acid) induce root formation; reverse levels induce bud formation. However, the effect of auxins in complicated and variable, the optimum of their concentration being very narrow. Furthermore, the presence of inhibitors and their disappearance at the time of flushing seems to have an important function (Sekawin, 1969).

Snow (1938) obtained up to 65 percent rooting of cuttings from one-year-old quaking aspen stump sprouts, if they were treated with 10 milligrams per liter of IBA indolebutyric acid) for 27 hours. Maximum rooting was obtained if cuttings were taken just before bud burst in spring. Barry and Sachs (1968) found that greenwood cuttings of quaking aspen taken from bud burst to mid-July rooted in varying degrees, depending on the collection date and on the concentration of IBA applied. High concentration (0.3 to 0.8 percent) stimulated rooting in April and May, whereas lower concentrations (0.1 percent) stimulated rooting in July. A sharp drop in rooting in June was correlated with rapid stem elongation on the donor trees.

Application of gibberellic acid ($GA_3$) in five different concentrations reduced the time of initiation and the number of suckers initiated on roots possessing few visible primordia. But it stimulated sucker outgrowth from roots which previously possessed large, visible primordia. Thus, $GA_3$ may interfere

with the first stage of adventitious shoot development, namely, meristem development (Schier, 1973c).

Clones - Clonal variation in the rooting of stem cuttings and in the development of suckers from root cuttings is frequently documented; it may be an interacting effect with date of collection (see above).

Strain (1964) found that root cuttings from two quaking aspen clones only 12 minutes of longitude apart differed in numbers and patterns of shoots produced. Based on field observations, reciprocal field garden tests, and common greenhouse studies, Strain pointed out that the aspen root cuttings taken from a clone on an exposed site had a higher potential for vegetative reproduction than cuttings from a non-exposed site clone. Barry and Sachs (1968) collected stem cuttings from several clones in the Sierra Nevada of California and in the Sierra de San Pedro Martin of Baja, California. None of the Sierra Nevada clones rooted, regardless of the IBA solution or Hormodin powder treatment applied, whereas hardwood cuttings taken in April from the Sierra de San Pedro Martin clone rooted 100 percent in all treatments. Maini (1967) found variation in the number of suckers and the date of initial suckering on root cuttings from four clones at 60, 75, and 85° (16, 24, and 29° C) but not at 95° F (35° C).

Moisture - Prevention of desiccation of either stem or root cuttings during propagation is prerequisite to success. An intermittent mist spray, maintaining an atmospheric relative humidity of about 80 to 90 percent (Sekawin, 1969) is common among investigators.

Nutrition - The metabolism of phosphorus and nitrogen and the C/N ratio seem to have an influence on the rooting of cuttings: while phosphorus stimulates rooting, nitrogen hinders it (Sekawin, 1969).

Age of the wood - Barry and Sachs (1968) stated that age of the wood is the most important factor affecting the rooting of quak-

ing aspen stem cuttings. Rarely is any success obtained on wood more than one year old.

Polarity - The number of suckers and buds formed on the proximal half of root cuttings is greater than that on the distal half of 10-cm-long segments. But new roots originated toward the distal end of the cuttings. This polarity is independent of light and gravity (Maini, 1968b). And Schier (1973a) found that vascular traces in all root segments studied turned toward the distal ends of the cuttings presumably because auxin is polarly transported toward the root apex.

Summary

In summary, quaking aspen is characterized by a pronounced capacity to form suckers from roots near the soil surface from pre-existing or currently-produced primordia. Sucker formation is normally released when the root system is severed from the stem. In the intact plant, suckering is partly or completely suppressed, presumably by factors active in apical dominance. There is evidence that auxin is important in inhibition of and formation and growth of suckers on aspen roots. An attractive hypotheses: auxin produced in the actively-growing shoots is translocated into the roots where it prevents sucker formation. When the aerial parts of the plant are removed or injured, root suckering is released as a response to lowered auxin concentration (Eliasson, 1969; 1971b). Sucker formation is initiated only under suitable temperature conditions (Maini and Horton, 1966b), and high light intensity is necessary to maintain the growth of new suckers (Sandberg and Schneider, 1953).

Artificially, quaking aspen can be propagated by several means, but most consistent success is obtained through the use of root cuttings. Most vigorous sucker production is obtained, if the cuttings are taken just prior to leaf flush, presumably before auxin inhibitors have been translocated to the roots. These suckers may then be severed and separately rooted.

## Introduction

Quaking aspen is an abundant species on many mountain sites in the West because of its response to forest fires. As an individ-tree, aspen has very low tolerance to the heat of a spreading fire, so mortality is usually high after a wildfire. A stand of aspen can be considered extremely tolerant to fire, however, and is almost certain to retain and even extend its range following fire. It is known as a "fire type," i.e., a species favored after fire because:

1. its roots are seldom damaged by fire;

2. the heat of the fire actually stimu-lates the generation of root suckers; and

3. most importantly, aspen stands usually do not support rapidly spreading or intense fires.

Since aspen occupies a wide variety of sites, the condition of the trees in a stand, the amount of dead and broken material beneath the stand, and hence the flammability, are extremely variable. Being deciduous, aspen's flammability also changes with the season. Some aspen stands are overmature, with the area characterized by moderate dead fuel volumes, standing snags, and open areas of brush or grass that present a potential for moderately high rates of fire spread and re-sistance to control. More typical is the thrifty stand with very little dead fuel below the trees, very little brush, and no ladder fuels to carry a potential fire to the crowns. This wide variation in flammability and its causes has not been quantified or comprehen-sively discussed in the literature. It is not well known on what sites or at what ages, or under what conditions, aspen is least flam-mable.

Typical healthy aspen stands have long been regarded by fire managers as relatively fireproof areas. Fire officers often con-struct control lines in aspen because the rate of spread and resistance to control are lower than in adjacent coniferous forests. Wild-fires spreading from high-elevation conifer-ous forests have been observed to die out with little or no suppression action in aspen stands. In Canada, firemen often attack the flanks of intense wildfires burning in spruce and attempt to "herd" the fire into aspen stands.

## Aspen as a Fuel Break

Some quantification of the usefulness of aspen as a fuelbreak can be achieved if generalizations are made. A fuelbreak of some kind might be considered wherever fuels are highly flammable and continuous, and where a high risk of fire ignition exists. Two examples of such a situation are dense stands of lodgepole pine or spruce-fir asso-ciations on steep topography around recrea-tional or residential communities in the Central Rocky Mountains. Either fuel complex can be described as fuel model G in the National Fire Danger Rating System (Deeming, et al., 1972). Fuelbreaks are useful under extreme burning conditions, i.e., low fuel moistures, high winds, and cured herbaceous vegetation. Under the worst possible con-ditions, fuel model G in the NFDR system would yield a spread component (SC) of 13, an energy release component (ERC) of 85, and a burning index (BI) of 58. Under the same conditions, an aspen stand, before leaf fall (NFDR fuel model H), would have a spread component of 8, an energy release component of 34 and a burning index of 27. Since the burning index is proportional to the effort to extinguish an initiating fire, it can be roughly estimated that the flammability of the aspen stand in this example is less than one-half that in the adjacent conifers. By comparison, flammability in a grass fuel-break might be only one-half that of aspen, as measured by burning index (Table 1), but fire spread would be much greater.

An important factor in evaluating the potential for large conflagrations is the possibility that the crows of trees will become involved in combustion, causing dis-tant spotting, very high energy release and frustrating fire control efforts. Studies in Rocky Mountain forests have shown that 34 percent of the fires that were crowning upon arrival f first suppression forces spread to Class C or larger size (Barrows, 1951). Mathematical techniques are available for estimating the rate-of-spread of fires in

Table 1 - Comparison of Burning Index (BI),
Energy Release Component (ERC),
and Spread Component (SC) in Three
Fuel Models of the National Fire-
Danger Rating System (Deeming, et
al., 1972) Under Extreme Burning
Conditions.

| Fuel Type | Model | SC | ERC | BI |
|-----------|-------|-----|-----|----|
| Dense Conifer | G | 13 | 85 | 58 |
| Aspen | H | 8 | 34 | 27 |
| Grass | A | 100 | 19 | 12 |

surface fuels (Rothermel, 1972). In the
absence of similar techniques for calculating
the mathematical probability that a fire will
crown it is necessary to use other methods
for evaluating this factor. Analysis of 151
crown fires showed the following general fuel
characteristics (Barrows, 1951):

| | Percent of Crown Fires |
|---|---|
| Dense coniferous forests with large volume of surface fuels | 38 |
| Dense coniferous forests with small volume of surface fuels | 30 |
| Open coniferous forests with large volume of surface fuels | 32 |

Other observations by fire experts have
provided a general ordinal ranking of crown-
ing potential (Fahnestock, 1970). This
scheme ranks the crowning potential of var-
ious forest stands on a scale of 0 to 10.
The dense conifer stands described above are
ranked 7 to 9. The crowning potential of
aspen stands is ranked near 0.

Fire experience has shown that crown
fires drop to the ground when they reach
quaking aspen stands, and prior to autumn
leaf fall, fire spreads only a short distance
in stands of this species. For example, on
the Jefferson Lake Fire (Pike National For-
est, Colorado) in July, 1974, fire spread
ceased within four meters after entering the
aspen from other fuel types. The Jefferson
Lake Fire is an excellent example of the
potential of aspen fuel breaks. The trees
along the edge of the aspen stands did
have the crown destroyed by the intense heat
of the fire (Figure 5) but the fire was
brought down to the ground. Once on the
ground the fire was stopped without any con-
trol activities by man (Figures 6, 7, 8).
The Wisconsin Department of Natural Resources
is presently establishing 1/4 mile wide hard-
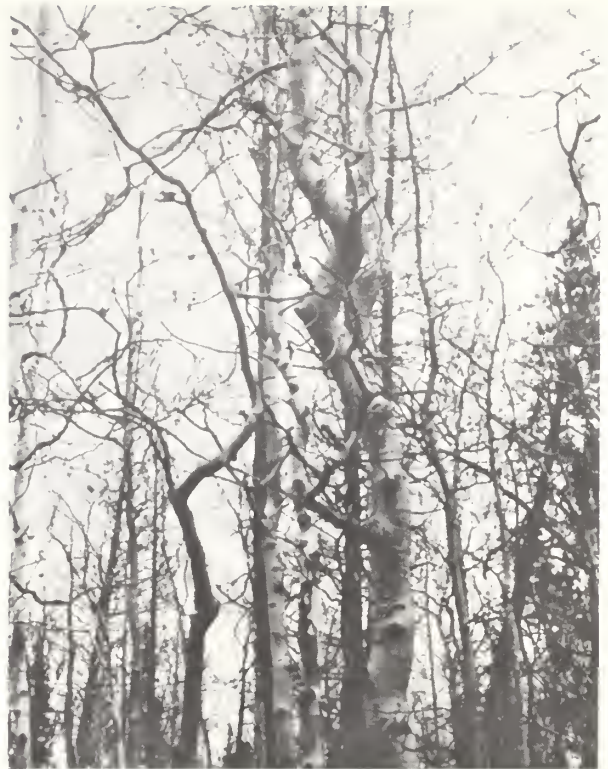wood fuel breaks in connection with timber
sales (Johnson, 1974).



Figure 5.--Aspen crown destroyed by intense
heat of fire.



Figure 6.--Aspen, a natural fire line.

Fire Analysis

The historic records of forest fires
in Colorado provide valuable information on
the occurrence and general behavior of fires
in a variety of forest types. Analyses of

Figure 7.--Ground fire stopped after burning 3 meters into a stand of aspen.



Figure 8.--Aspen, an effective fuel break.

these records permit comparisons of fire performance in aspen and other forest types.

One of the earliest references to aspen and its resistance to fire is found in the report of a 1929 burn that occurred on Twin Sisters Peak in Rocky Mountain National Park (U.S. National Park Service, 1916-1974). This burn, known as the Butterfly Fire, occurred on June 24, 1929, and swept over some 72 acres of lodgepole pine and aspen. The report states: "The fire progressed mainly in the pines, going around the stands of aspen." Recent fire ecology studies of the burn show the continued growth of aspen on the site (Clagg, 1975).

The individual fire reports prepared by the U.S. Forest Service provide extensive data on fire characteristics. Computer aided analysis have been made of 4590 fires occurring in the National Forests of Colorado during the 14-year period 1960-1973 (Ryan and Barrows, 1975). The available data permits stratification of each fire according to the prevailing forest cover type at the site (Tables 2 and 3). In the fire reporting system for the National Forests all fires in deciduous species are grouped in a single forest cover type classification. Virtually all of the fires reported in the deciduous type are in aspen. The only exception may be an occasional fire in cottonwood or willows. We have concluded that our studies of 215 fires listed on fire reports as occurring in the deciduous cover type represents an accurate description of aspen fires.

Fire Occurrence

During the 1960-1973 period, in the Colorado National Forests, 215 of a total of 4590 fires or 4.7 percent occurred in deciduous (primarily aspen) forests (Table 2). In comparison to the coniferous forests and to the brush and grass cover types fire occurrence in aspen is very low. Fires in coniderous forests accounted for 83.6 percent and those in brush and grass for 9.9 percent of the fire ignitions.

In examination of fire ignition rates for various forest cover types, it is essential to consider the source of ignition and in turn the general character of the fire igniting brand. A special study in the Front Range National Forests showed that fires in aspen stands were 84 percent man-caused and only 16 percent lightning-caused. The average annual ignition rate per million acres for aspen was 9.7 man-caused fires and 1.9 lightning fires. Aspen stands were the least ignitable by lightning of any Colorado forest cover type. The man-caused ignition rates were slightly higher in aspen than in spruce-fir and pinyon-juniper types (Table 4).

A study of fire occurrence in aspen stands on all Colorado national forests during 1960-1973 showed ignitions in every month except February. The total annual average fire occurrence in aspen for all ten national forests was less than two fires per month for every month except July, August, and October. The peak ignitions during these months probably reflect combinations of severe fire

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Table 2　Fire occurrence by Forest Cover Type and Size
Class, Colorado National Forests, 1960-1973.
(Basis 4590 Fires)

| Forest cover type | No and percent | Size class of fire | | | | | | Total |
| | | A | B | C | D | E | F | |
|---|---|---|---|---|---|---|---|---|
| Deciduous (primarily aspen) | # | 161 | 40 | 12 | 2 | 0 | 0 | 215 |
| | % | 74.9 | 18.6 | 5.6 | 0.9 | | | 4.7 |
| Ponderosa pine | # | 1462 | 425 | 27 | 1 | 2 | 1 | 1918 |
| | % | 76.2 | 22.2 | 1.4 | 0.1 | 0.1 | 0.1 | 41.7 |
| Lodgepole pine | # | 391 | 80 | 7 | 4 | 2 | 1 | 485 |
| | % | 80.6 | 16.5 | 1.4 | 0.8 | 0.4 | 0.2 | 10.6 |
| Spruce -- fir | # | 511 | 63 | 13 | 4 | 3 | 1 | 595 |
| | % | 85.8 | 10.6 | 2.2 | 0.7 | 0.5 | 0.2 | 12.9 |
| Douglas-fir | # | 341 | 50 | 5 | 1 | 0 | 0 | 397 |
| | % | 85.9 | 12.6 | 1.3 | 0.3 | | | 8.6 |
| Subalpine fir | # | 252 | 26 | 3 | 1 | 0 | 0 | 282 |
| | % | 89.4 | 9.2 | 1.1 | 0.4 | | | 6.1 |
| Pinyon -- juniper | # | 130 | 19 | 7 | 2 | 2 | 0 | 160 |
| | % | 81.3 | 11.9 | 4.4 | 1.3 | 1.3 | | 3.5 |
| Total conifers | # | 3087 | 663 | 62 | 13 | 9 | 3 | 3837 |
| | % | 80.5 | 17.3 | 1.6 | 0.3 | 0.2 | 0.1 | 83.6 |
| Heavy brush | # | 46 | 30 | 7 | 1 | 0 | 0 | 84 |
| | % | 54.8 | 35.7 | 8.3 | 1.2 | | | 1.8 |
| Grass -- sage | # | 280 | 131 | 37 | 6 | 0 | 0 | 454 |
| | % | 61.7 | 28.9 | 8.1 | 1.3 | | | 9.9 |
| Total brush -- grass | # | 326 | 161 | 44 | 7 | 0 | 0 | 538 |
| | % | 60.6 | 29.9 | 8.2 | 1.3 | | | 11.7 |
| Total all types | # | 3574 | 864 | 118 | 22 | 9 | 3 | 4590 |
| | % | 78.0 | 18.8 | 2.6 | 0.5 | 0.2 | 0.1 | |

Table 3.  Analysis of Area Burned and Occurrence
of Class C or Larger Fires by Forest
Cover Types in Colorado National
Forests, 1960-1973.  (Basis 4590 fires)

| Forest cover type | Total acres burned | Percent of total acres burned | Average acres burned per fire | Percent of fires in type, Class C or larger |
|---|---|---|---|---|
| Deciduous (primarily aspen) | 766 | 3.93 | 3.563 | 6.51 |
| Ponderosa pine | 4966 | 25.49 | 2.489 | 1.62 |
| Lodgepole pine | 4813 | 24.70 | 9.924 | 2.89 |
| Spruce -- fir | 3605 | 18.50 | 6.059 | 3.53 |
| Douglas-fir | 525 | 2.69 | 1.322 | 1.51 |
| Subalpine fir | 313 | 1.61 | 1.110 | 1.42 |
| Pinyon -- juniper | 1606 | 8.24 | 10.037 | 6.87 |
| Total conifers | 15,828 | 81.24 | 4.125 | 2.27 |
| Heavy brush | 365 | 1.87 | 4.345 | 9.52 |
| Grass -- sage | 2525 | 12.96 | 5.562 | 9.47 |
| Total brush -- grass | 2890 | 14.83 | 5.372 | 9.48 |
| Total all Types | 19,484 | | 4.245 | 3.31 |

weather, cured conditions for aspen leaves
and surface vegetation and human fire-causing
activity.  The total fire occurrence in aspen
by month during the 14-year period was as
follows:

| | | | | | |
|---|---|---|---|---|---|
| January | 1 | May | 19 | September | 18 |
| February | 0 | June | 24 | October | 48 |
| March | 1 | July | 43 | November | 1 |
| April | 8 | August | 45 | December | 7 |

Table 4. Number of Fires Per Million Acres By Cause
and Forest Cover Type, Colorado Front Range
National Forests, (a) 1960-1969.
(Basis 1573 fires)

| Forest cover type | Lightning fires | Man-caused fires | Total fires |
|---|---|---|---|
| Deciduous (primarily aspen) | 1.9 | 9.7 | 11.6 |
| Ponderosa pine | 81.9 | 50.1 | 132.0 |
| Lodgepole pine | 8.3 | 14.4 | 22.7 |
| Spruce -- fir | 4.1 | 9.2 | 13.3 |
| Douglas-fir | 25.5 | 15.9 | 41.4 |
| Other cover types (b) | 3.6 | 8.6 | 12.2 |
| Total all types | 13.0 | 13.9 | 26.9 |

(a) Arapaho, Pike, Rio Grande, Roosevelt and San Isabel
National Forests.
(b) Pinyon-juniper, Heavy-brush, Grass-sage and Sub-Alpine
types.

Size Class of Fire

The potential for fires to spread to
large sizes provides one means for evaluat-
ing fuel flammability in various forest cover
types. In Colorado national forests 78.0
percent of the fires in all cover types spread
to less than one-fourth acre in size (Class A)
during the 1960-1973 study period (Table 2).
In coniferous forests the smallest percentage
of fires spread beyond Class A size while
the largest percentage was in brush-grass
cover types. Fires in aspen stands were
between these two extremes. These figures
reflect potential initial rates-of-fire spread.
Fires in cured vegetation and dry leaves de-
posited to the ground from deciduous trees
may be expected to have higher initial rates
of spread than in the shaded duff and light
litter fuels of coniferous forests.

Fires in aspen stands have limited poten-
tial to spread to sizes of more than 100 acres
(Class D or larger). In the national forests

of Colorado only 2 aspen fires reached Class
D size during the 1960-1973 period. None of
the 12 fires greater than 300 acres in size
were in aspen. The average annual occurrence
rate of Class D or larger fires per million
acres in aspen stands is 0.30 as compared to
0.43 for all other cover types. All of the
larger fires in aspen (both Class C and D)
occurred in August or later in the year.

Area Burned

Our studies showed that 766 acres were
burned in aspen stands during the 14-year
period. This is 3.93 percent of the total of
19,484 acres burned during the period in
Colorado national forests (Table 3). The
average size per fire was 3.56 acres in aspen
as compared to 4.12 acres in coniferous
forests and 5.37 acres in brush-grass types.
The average annual area burned per million
acres was 28.2 acres in aspen as compared to
157.9 acres for all types. Aspen has the
lowest acreage burned per unit area of any
cover type in the Colorado national forests.

Fire Analysis Summary

The overall analysis of fires shows that aspen has a relatively low fire potential in comparison to other cover types in Colorado. Lightning fire ignition rates are the lowest of any forest type and overall ignition rates are less than half the rate for all cover types. Moderate fire spread rates are possible in some aspen stands especially when cured and dry conditions occur in leaves and understory vegetation. Low surface fuel volumes and the absence of crown fire potential make high energy fires unlikely. Some exceptions to these factors may occur in old aspen stands containing larger amounts of dead and downed fuels. Site factors, limited areas of large and continuous stands and low to moderate levels of fuel flammability restrict the probability of large fires developing in aspen stands. It should be emphasized, however, that unsuppressed fires in aspen can spread into other cover types having a higher potential for burning large areas.

### Fuel Break Specifications and Recommendations

The use and management of aspen stands for fuel break purposes appears to be a promising opportunity on selected mountain sites in Colorado. As aspen fuel break program should involve the management of natural stands and the propagation of new stands.

Location of Fuel Breaks

The location of fuel breaks requires consideration of fire ignition and behavior factors, characteristics of major fuel bodies in the area, value of resources and developments to be protected, landscape aesthetics, soil and climate features of the site, topography and probability for enhancing specific types of fire suppression operations. Ideally, from a fire viewpoint, fuel breaks should serve one or more of the following functions:

1. Provide an area of low fuel flammability at or near the sites of likely fire ignitions.

2. Prevent initiating fires from spreading rapidly either to dangerous fuel and topographic situations or to high value sites.

3. Provide an environment favoring application of suppression operations that will stop the spread of fires.

In Colorado mountain country, fuel breaks can best aid fire fighting when located at or near the base of slopes, along ridge tops, along lateral ridges, in low mountain passes or saddles and at major changes from steep to gentle topography. In some situations fuel breaks are useful when located in the middle of steep mountain slopes. Fuel breaks at such locations must be extensive to prevent fires from either running through them or spotting over them. Fuel breaks along roads in steep mountain topography can facilitate fire suppression. Fuel breaks located around resorts, recreation areas, industrial sites and other areas having a high potential for man-caused fires can serve both fire prevention and fire suppression functions.

Width of Fuel Breaks

In the design of fuel breaks, major consideration must be given to the critical dimensions necessary for stopping the spread of a fire. The fire spread may occur by continuous advance through surface fuels, crowning or spotting ahead. Normally, fire spread is not expected to be fully stopped by the fuel break itself. The fuel break provides an environment to slow doen fire spread, minimize spotting and crowning, and facilitate fire suppression. The complete stopping of fire spread in a fuel break almost always requires fire suppression action and mop-up. All of these factors are related to fuel break width.

It is not possible to establish a standard width for all fuel breaks. Questionnaires and interview responses from fire control officers in Forest Service Regions 1 and 2 revealed a wide variation in recommended fuel break dimensions. The concensus of opinion was that the width of the fuel break would be dependent on topography, fire potential of the area and the type of adjoining fuels. In general they recommended a width of 20 to 100 meters.

Additional research is needed to develop more specific recommendations for the width of aspen fuel breaks under a variety of topographic and fuel situations. Tests are needed of this hypothesis: "Fuel break width is governed by interrelated factors of (1) burning characteristics of surrounding vegetation, (2) burning characteristics of fuel break vegetation, (3) steepness of slope and (4) topographic position of the fuel break." Testing of this hypothesis will be a complex matter requiring specific experiments and analyses of wildfire behavior.

## Fuel Break Management

Fuel break management involves treatment of both natural aspen stands and new stands propagated for fire control purposes. Many natural stands may be located on sites where they can serve as fuel breaks. These sites can be enhanced through application of management techniques.

One of the most important management techniques for aspen stands is the timely application of prescribed fire. Reduction of surface fuel flammability can be achieved through use of low intensity fires. These fires can reduce accumulations of light litter, dead limb wood and dry leaves. In addition, low intensity prescribed fires can foster the continued propagation of aspen stands by stimulating the generation of root suckers. Management operations in older stands may also require the physical removal of standing snags.

Newly propagated stands of young aspen may be vulnerable to fire. Mortality to small trees may be expected especially where there is an accumulation of surface fuels. For these reasons prescribed fire should be applied prior to operations for the propagation of new stands.

A prescribed fire program should be initiated in selected aspen stands and at proposed sites for establishment of aspen fuel breaks in Colorado forests.

The effect of quaking aspen stands in minimizing fire initiation, in bringing crown fires down to the surface, and in slowing and eventually stopping the spread of surface fires is well documented. Tentative recommendations for width and frequency of aspen stands for fuelbreaks are in the minds of field personnel.

Quaking aspen has been propagated successfully in the laboratory, and its sprouting has been successfully encouraged in natural stands. But the potential for establishing new stands of quaking aspen on sites where it has not been previously established has not been investigated. Also the clonal variation at different altitudes is not well understood.

The following recommendations are made:

1. That research be initiated on the artificial establishment of quaking aspen stands as fuelbreaks.

2. That such research continue for no less than three years and consist of both laboratory-greenhouse and field phases.

3. That collection of material for propagation in such research be widely-spread as to altitudinal clone source.

4. That field experiments and wildfire analysis be performed to establish specifications for widths and locations of aspen fuel breaks.

5. That prescribed fire research be initiated to establish and test fire management guidelines for aspen stands.

LITERATURE CITED

Baker, Frederick S.
    1918.  Aspen reproduction in relation to
        management.  Jour. For. 16(4): 389-398.

Baker, Frederick S.
    1921.  Two races of aspen.  Jour. For. 19
        (4): 412-413.

Barnes, Burton V.
    1966.  The clonal growth habit of American
        aspen.  Ecology 47(3): 439-447.

Barrows, Jack S.
    1951.  Forest fires in the Northern Rocky
        Mountains.  U. S. Dep. Agric., For.
        Serv. Stn Paper 28.  251 p.  Northern
        Rocky Mt. For. and Range Exp. Stn.
        Missoula, Mont.

Barry, W. J. and R. M. Sachs.
    1968.  Vegetative propagation of quaking
        aspen.  Calif. Agric. 22: 14-16.

Benson, Miles K. and Duane Dubey.
    1972.  Aspen seedling production in a com-
        mercial nursery.  Gen. & Phys. Note
        No. 12.  Institute of Paper Chemistry,
        Appleton, Wis.

Blackburn, Kathleen B. and J. W. Heslop
    Harrison.
    1924.  A preliminary account of the chro-
        mosomes and chromosome behavior in the
        Salicaceae.  Ann. Bot. 38: 361-378.

Blake, G. M., R. L. Hossfeld, and S. S. Pauley.
    1960.  A technique for determining sex
        from vegetative buds of quaking aspen.
        For. Sci. 6(4): 363-364.

Blake, G. M., R. L. Hossfeld, and S. S. Pauley.
    1967.  More on the determination of sex
        from the vegetative buds of aspen.
        For. Sci. 13(1): 89.

Brown, A. B.
    1935.  Cambial activity, root habit and
        sucker shoot development in two species
        of poplar.  New Phytol. 34(3): 163-179.

Canadian Forestry Service.
    1974.  The familiar poplar.  Forestry Rep.
        4(1): 3.  Edmonton, Alberta.

Clagg, Harry B.
    1975.  Fire ecology in high elevation
        forests in Colorado.  Colo. State
        Univ.  MS thesis.

Deeming, J. D., J. W. Lancaster, M. A. Fosberg,
    R. W. Furman, and M. J. Schroeder.
    1972.  National fire-danger rating system.
        USDA For. Serv. Res. Paper RM-84.  165
        p.  Rocky Mt. For. and Range Exp. Stn.,
        Fort Collins, Colo.

Einspahr, Dean W.
    1960a.  Abnormal flowering behavior in
        aspen.  Iowa State Jour. Sci. 34(4):
        623-630.

Einspahr, Dean W.
    1960b.  Sex ratio in quaking aspen and
        possible sex related characteristics.
        Fifth World Forestry Congress.
        Seattle, Wash.

Eliasson, Lennart.
    1969.  Growth regulators in Populus tremula
        I.  Distribution of auxin and growth
        inhibitors.  Physiol. Plant. 22(6):
        1288-1301.

Eliasson, Lennart.
    1971a.  Growth regulators in Populus tre-
        mula II.  Effect of light on inhibitor
        content in root suckers.  Physiol.
        Plant. 24(2): 205-208.

Eliasson, Lennart.
    1971b.  Growth regulators in Populus tre-
        mula III.  Variation of auxin and in-
        hibitor level in roots in relation to
        root sucker formation.  Physiol. Plant.
        25(1): 118-121.

Eliasson, Lennart.
    1971c.  Growth regulators in Populus tremula
        IV.  Apical dominance and suckering in
        young plants.  Physiol. Plant. 25(2):
        263-267.

Ellison, Lincoln.
    1943.  A natural seedling of western aspen.
        Jour. For. 41(10):  767-768.

Erlanson, Eileen Whitehead and Frederick Hermann.
    1927.  The morphology and cytology of perfect
        flowers in Populus tremuloides Michx.
        Papers of the Mich. Acad. Sci., Arts, and
        Letters 8:  97-110.

Fahnestock, B. G.
    1970.  Two keys for appraising forest fire
        fuels. USDA For. Serv. Res. Pap. PNW-99.
        26 p. Pacific Northwest For. and Range
        Exp. Stn., Portland, Ore.

Farmer, Robert E.
    1962.  Aspen root sucker formation and apical
        dominance.  For. Sci. 8(4): 403-410.

Farmer, Robert E.
    1963. Vegetative propagation of aspen by
        greenwood cuttings. Jour. For. 61(5):
        385-386.

Fechner, Gilbert H.
    1972. Development of the piltillate flower
        of Populus tremuloides following controlled
        pollination. Canad. Jour. Bot. 40(12):
        2503-2509.

Fechner, Gilbert H.
    1975. Development of unpollinated ovules of
        quaking aspen. Proceedings: Northeastern
        Forest Tree Improvement Conference. New
        Brunswick, New Jersey. August 5-7. In Press

Fowells, H. A.
    1965. Silvics of forest trees of the United
        States. Agric. Handbk. 271. U.S. Dep.
        Agric., Washington, D.C.

Gifford, Gerald F.
    1966. Aspen root studies on three sites in
        northern Utah. Amer. Mic. Nat. 75(1):
        132-141.

Heimburger, C.
    1951. Report on forest tree breeding: poplar.
        Progress Report. Field Laboratory Project.
        Ont. Dept. of Lands and Forests. Forestry
        Asbtracts.

Horn, Arthur G.
    1954. Aspen makes up nearly one-half of 1953
        pulpwood cut in Lake States. Tech. Note
        418. Lake States For. Exper. Stn. St.
        Paul, Minnesota.

Johnson, Von J.
    1974. Fire Working Group. Society of Amer-
        ican Foresters National Convention.

Johnsson, Helge.
    1940. Cytological studies of diploid and
        triploid Populus tremula and crosses
        between them. Hereditas 26(3,4): 321-352.

Jones, John R.
    1974a. Aspen sucker growing from an Engel-
        mann spruce stump. USDA For. Serv. Res.
        Note RM-264. Rocky Mt. For. and Range
        Exp. Stn. Fort Collins, Colo. 2 p.

Jones, John R.
    1974b. Silviculture of southwestern mixed
        conifers and aspen: the status of our
        knowledge. USDA For. Ser. Res. Pap.
        RM-122. Rocky Mt. For. and Range Exp.
        Stn. Fort Collins, Colo. 44 p.

Jones, John R.
    1967. Aspen site index in the Rocky Moun-
        tains. Jour. For. 65(11): 820-821.

Kozlowski, T. T.
    1971a. Growth and development of trees.
        Vol. I. Academic Press. New York. 443 p.

Kozlowski, T. T.
    1971b. Growth and development of trees.
        Vol II. Academic Press. New York. 514 p.

Kramer, Paul J. and Theodore T. Kozlowski.
    1960. Physiology of trees. McGraw-Hill
        Book Co., Inc. New York. 642 p.

Larson, Philip R.
    1958. Effect of gibberellic acid on forcing
        hardwood cuttings for pollen collection.
        Tech. Note 538. Lake States For. Exp.
        Stn. St. Paul, Minnesota.

Lester, Donald T.
    1963. Floral initiation and development in
        quaking aspen. For. Sci. 9(3): 323-329.

Maini, J. S.
    1967. Variation in the vegetative propaga-
        tion of Populus in natural populations.
        Bull. Ecol. Soc. Amer. 48(2): 75-76.

Maini, J. S.
    1968a. Silvics and ecology of Populus in
        Canada. In Growth and Utilization of
        poplars in Canada. Forestry Branch Publ.
        No. 1205: 20-69. Dept. of Forestry and
        Rural Development. Ottawa, Ontario.

Maini, J. S.
    1968b. The relationship between the origin
        of adventitious buds and the orientation
        of Populus tremuloides root cuttings.
        Bull. Ecol. Soc. Amer. 49(2): 81-82.

Maini, J. S. and R. T. Coupland.
    1964. Anomolous floral organization in
        Populus tremuloides. Canad. Jour. Bot.
        42: 835-849.

Maini, J. D. And K. W. Horton.
    1966a. Reproductive response of Populus
        and associated Pteridium to cutting,
        burning, and scarification. Dept.
        Publ. No. 1155. Dept. of Forestry and
        Rural Development. Ottawa, Ontario.

Maini, J. D. and K. W. Horton
    1966b. Vegetative propagation of Populus
        spp. I. Influence of temperature on
        formation and initial growth of aspen
        suckers. Can. Jour. Bot. 44(9): 1183-
        1189.

Mathes, Marin C.
    1964. The culture of isolated triploid
        aspen tissue. For. Sci. 10(1): 35-38.

Miller, Robert L. and Grover A. Choate.
1964. The forest resource of Colorado.
U. S. For. Serv. Res. Bull. INT-3.
Intermt. For. and Range Exp. Stn.
Ogden, Utah. 54 p.

Morgan, M. D.
1969. Ecology of aspen in Gunnison
County, Colorado. Amer. Mid. Nat.
82(1): 204-228.

Moss, E. H.
1938. Longevity of seed and establishment
of seedlings in species of Populus.
Bot. Gaz. 99(3): 529-542.

Moss, E. H.
1960. Spring phenological records at
Edmonton, Alberta, Can. Field-Nat.
74(2): 113-118.

Nagaraj, M.
1952. Floral morphology of Populus
deltoides and P. tremuloides.
Botanical Gazette 114: 222-243.

Pauley, Scott S.
1949. Forest-tree genetics research:
Populus L. Econ. Bot. 3(3): 299-330.

Pauley, Scott S.
1948. Sex and vigor in Populus. Science
108: 302-303.

Pauley, Scott S. and George F. Mennel.
1957. Sex ratio and hermaphroditism in
a natural population of quaking aspen.
Minn. For. Note No. 55. Univ. Minn.
St. Paul, Minnesota.

Pauley, Scott S. and Thomas O. Perry.
1954. Ecotypic variation of the photo-
periodic response in Populus. Jour.
Arnold Arbor. 35(2): 167-188.

Perala, Donald A.
1974. Prescribed burning in an aspen-
mixed hardwood forest. Can. Jour.
For. Res. 4(2): 222-228.

Perry, T. O. 1971. Dormancy of trees in
winter. Science 171 (3966): 29-36.

Peto, F. H.
1938. Cytology of poplar species and
natural hybrids. Canad. Jour. Res.
Sect. C 16(11): 445-455.

Reed, Robert M.
1971. Aspen forest of the Wind River
Mountains, Wyoming. Amer. Midl.
Nat. 86(2): 327-343.

Rehder, Alfred.
1940. Manual of cultivated trees and
shrubs hardy in North America. The
Macmillan Co. New York.

Rothermel, Richard C.
1972. Mathematical model for predicting
fire spread in wildland fuels. Inter-
mountain Forest and Range Exp. Stn.
Ogden, Utah. 54 p.

Ryan, Kevin C. and Jack S. Barrows.
1975. Analysis of fire hazards and risks
in Front Range forests of Colorado.
Colo. State Univ. Res. Report.

Sandberg, Dixon and Arthur E. Schneider.
1953. The regeneration of aspen by
suckering. Minn. For. Note No. 24.
Univ. Minn. St. Paul, Minnesota.

Santamour, F. S.
1956. Hermphroditism in Populus.
Proceedings Third Northeastern Forest
Tree Improvement Conference. Ithaca,
New York. 1955.

Schier, George A.
1972. Apical dominance in multishoot
cultures from aspen roots. For. Sci.
18(2): 147-149.

Schier, George A.
1973a. Origin and development of aspen
root suckers. Canad. Jour. For. Res.
3: 45-53.

Schier, George A.
1973b. Seasonal variation in sucker pro-
duction from excised roots of Populus
tremuloides and the role of endogenous
auxins. Can. Jour. For. Res. 3(3):
459-461.

Schier, George A.
1973c. Effects of gibberellic acid and
an inhibitor of gibberellin action on
suckering from aspen root cuttings.
Can. Jour. For. Res. 3(1): 39-44.

Schier, G. A. and J. C. Zasada.
1973. Role of carbohydrate reserves in
the development of root suckers in Pop-
ulus tremuloides. Can. Jour. For.
Res. 3(2): 243-250.

Schlenker, Gerhard.
1953. Beobachtungen über die Geschlech-
tsverhältnisse bein Graupappeln und
Äpsen. Zeitschrift für Forstgenetik
und Forstpflanzenzüchtung 2(5):
102-104.

Seitz, F. W.
   1958. Früntreibversuche mit Blühreisern der Aspe. Silvae Genetica 7(3): 102-105.

Seitz, F. W.
   1953. Über anomale Zwitterblüten eines Klones der Gattung Populus, Sektion Leuce. Zeitschrift für Forstgenetik und Forstpflanzenzüchtung 2(4): 77-90.

Sekawin, M.
   1969. La propagation due peuplier. Second world consultation on forest tree breeding. Washington, D. C. English summary.

Shirley, Hardy L.
   1931. Does light burning stimulate aspen suckers? Jour. For. 29(4): 524-525.

Shirley, Hardy L.
   1932. Does light burning stimulate aspen suckers? II. Jour. For. 30(4): 419-420.

Smith, E. Chalmers.
   1943. A study of cytology and speciation in the genus Populus L. Jour. Arn. Arbor. 24(3): 275-305.

Snow, Albert G., Jr.
   1938. Use of indolesbutyric acid to stimulate the rooting of dormant aspen cuttings. Jour. For. 36(6): 582-587.

Starr, G. H.
   1971. Propagation of aspen trees from lateral roots. Jour. For. 69(12): 866-867.

Stettler, Reinhard F.
   1966. Sex expression in Populus trichocarpa (T. & G. ex Hook.) and in its hybrids. Proceedings, Western Forest Genetics Association, 1965. Olympia, Washington.

Stoeckler, Joseph H.
   1960. Soil factors affecting the growth of quaking aspen forests in the Lake States. Tech. Bull. 233. Agric. Exp. Stn. Univ. Minn. St. Paul, Minnesota.

Strain, Boyd Ray.
   1964. Physiological and morphological variability of local quaking aspen clones. PhD dissertation. Univ. Calif. of Los Angeles. Los Angeles, Calif. 156 p.

Strothman, R. O. and Z. A. Zasada.
   1957. Silvical characteristics of quaking aspen. Sta. Pap. No. 49. Lake States For. Exp. Stn., St. Paul, Minn. 26 p.

U. S. National Park Service.
   1916-1974. Fire reports and fire atlas. On file at Rocky Mountain Nat'l. Park.

U. S. Forest Service. Coding instructions for individual fire reports. Rocky Mountain Region, Denver, Colo.

Vartaaja, O.
   1960. Ecotypic variation of the photoperiodic response in trees especially in two Populus species. For. Sci. 6(3): 200-206.

Winton, Lawson L.
   1968a. The initiation of friable aspen callus. Phyton 25(1): 15-21

Winton, Lawson L.
   1968b. Initiation of friable aspen callus under different light environments. Phyton 25(1): 23-28.

Winton, Lawson L.
   1968c. The rooting of liquid-grown aspen callus. Amer. Jour. Bot. 55(2): 159-167.

Winton, Lawson L.
   1970. Shoot and tree production from aspen tissue culture. Amer. Jour. Bot. 57(8): 904-909.

Zasada, John C. and George A. Schier.
   1973. Aspen root suckering in Alaska: Effect of clone, collection date, and temperature. Northwest Sci. 47(2): 100-104.

Zimmermann, Martin H. and Claud L. Brown.
   1971. Tree structure and function. Springer-Verlag, New York. 336 p.

Zufa, L.
   1971. A rapid method for vegetative propagation of aspens and their hybrids. For. Chron. 47(1): 36-39.